A MIOCENE SOLENOPOROID ALGA SHOWING REPRODUCTIVE STRUCTURES

by GRAHAM F. ELLIOTT

ABSTRACT. The Miocene alga *Neosolenopora armoricana* sp. nov. is described. It is most exceptional amongst Solenoporaceae in showing clear reproductive structures interpreted as similar to Corallinacean asexual sporangia, single and fused; a possible sexual structure is also described. This development came at the very end of solenoporacean evolution.

SOLENOPORACEAE are fossil calcareous algae, believed wholly extinct, which range in geological time from lower Palaeozoic to mid-Tertiary. In some ways their structure resembles that of the more familiar Corallinaceae, which especially characterize the Tertiary and of which living examples abound in present-day seas, and it seems likely that some solenoporaceans were ancestral to the corallines.

In one character the two groups differ sharply. Reproductive bodies in the Corallinaceae leave conspicuous and common structures in the fossils, so giving evidence of evolution and affording most useful morphological detail for classification. By contrast, in the Solenoporaceae, definite reproductive structures are usually missing. Those evidences interpreted as reproductive traces are usually very doubtful, so that there are very few indeed intrinsically recognizable as reproductive, and those are not found in most individuals of the relevant species. It has been supposed that reproductive structures were external and not calcified (Pia 1927, p. 97).

Many workers on fossil algae have, however, described alleged solenoporacean calcified reproductive structures and discussed the problem of their usual absence. Useful reviews of previous work are those of Wood (1944) and in Elliott (1965).

The present note describes a solenoporacean which shows definite reproductive structures with some evidence of their individual development. This is then discussed in relation to the evolution of the family. The specimens described were collected by Mr. L. J. Pitt amongst bryozoan material. The late Dr. H. D. Thomas, recognizing them as anomalous, consulted me and they were provisionally identified as a species of *Neosolenopora*, but not studied in detail until now.

Class RHODOPHYCEAE (Red Algae)
Order CRYPTONEMIALES
Family SOLENOPORACEAE
Genus NEOSOLENOPORA Mastrorilli 1955

Type-species. N. patrinii Mastrorilli 1955 (*Solenopora vinassai* (Patrini) Mastr., *non S. vinassai* Vialli 1938); Miocene of Italy.

Diagnosis (emend. Elliott). Solenoporaceae with rudimentary hypothallus, typical solenoporacean septate-tubular perithallus, and zonal development of reproductive cavities mostly formed by fusion of smaller reproductive elements.

Range. Miocene.

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Neosolenopora armoricana sp. nov.

Plates 21–22

1965 *N. patrinii* Mastrorilli; Elliott, p. 699, pl. 108, figs. 1, 2.

Diagnosis. Neosolenopora with cell-columns (tubules) of about 0·09 mm diameter, cells varying in length from 0·05 to 0·20 mm. Oval reproductive bodies about 0·18 mm high and 0·11 mm diameter, typically fused into aggregates of up to 0·60 mm diameter.

Description. This alga is preserved as near-spherical or ovoid growths up to 20 mm high and 30 mm maximum diameter. The lower surface shows a scar or area of original attachment. The growths are often crusted with organic debris, including molluscan and echinoid fragments, and they may show surface growths of bryozoa. A clean outer surface shows a pattern of adjacent fine circular apertures, separated by gently convex calcareous skeletal material. Worn or broken surfaces show indications of the structures described below from thin-sections.

In thin-section the internal structure is seen to be typically solenoporoid. Banding or zonation is present, but is not nearly so marked as in many other solenoporoids. Fairly close-packed tubules or cell-columns, usually gently curved, radiate from the basal area to the exterior, where their terminations show as the circular apertures of the outer surface. The tubules are circular in cross-section, not usually adpressed, and divided by conspicuous wall-material which may be thickened at certain points. The diameter of the tubules, mid-wall to mid-wall, is about 0·091 mm (0·082–0·109 mm seen); the internal diameter varies from 0·073 to 0·082 mm. The thickness of the wall-material between two adjacent tube-cavities varies from 0·009 to 0·027 mm; it does not show as a double structure even under a high magnification.

In vertical section the thickening of wall-material, apart from slight irregularity, is seen to occur mostly at changes in direction (curvature) of the tubules, often near the exterior. Mostly the tubules run adjacent and parallel, but what seems to be intercalation, and more rarely, bifurcation, occurs sparingly and randomly in the main thickness. The tubules are divided into chambers by frequent thin septa, usually gently concave with the curvature pointing inwards, i.e. away from the exterior. They may, however, be quite flat, set either at right angles to the walls or obliquely. Septa in adjacent tubules may be at the same level across several tubules, but there is no regularity at all in this occurrence, chamber-length varying from 0·054 to 0·200 mm. The septa are about 0·004–0·009 mm thick; the observed differences in this may well be mostly due to preservation.

In vertical section the tubules are seen to originate horizontally at the base of the growth, and then turn fairly sharply upwards, broadening in diameter and becoming typically septate. This basal portion is interpreted as a rudimentary hypothallus. It is not the same as the markedly distinct hypothallus (as opposed to perithallus) which occurs in many members of the Corallinaceae. Whether different preservation and different orientation of section of this rudimentary hypothallus would give a picture like the basal structures, interpreted as hypothallus, in *Cretacicrusta* (Elliott 1972) and *Solenopora* cf. *nigra* Brown (Öpik and Thomson 1933) is not known.

The main thickness of the growths contains various cavities, which are not part of the original plant structures. They are usually though not invariably irregular in outline, wholly or partly calcite-filled, and may be due to accident, borings made from the exterior, debris included during growth in life, or differential diagenesis. As well as these, however, there occur various rounded cavities, of similar calcite filling to the others, but each bounded by a definite organic wall. In vertical section they are seen to occur in curved

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EXPLANATION OF PLATE 21

Figs. 1–4. *Neosolenopora armoricana* sp. nov. Miocene, Vindobonian, Savignéan Falun; La Perchais Quarry, Tréfumal, south of Dinan, Brittany, France. 1, 2, Thin-sections; vertical and transverse sections of radiate cell-columns, ×46. V. 53652c, V. 53652b. 3, Portion of exterior of solid algal growth, ×30. V. 57125. 4, Thin-section, vertical cut to show row of reproductive bodies, ×46. V. 53652c.

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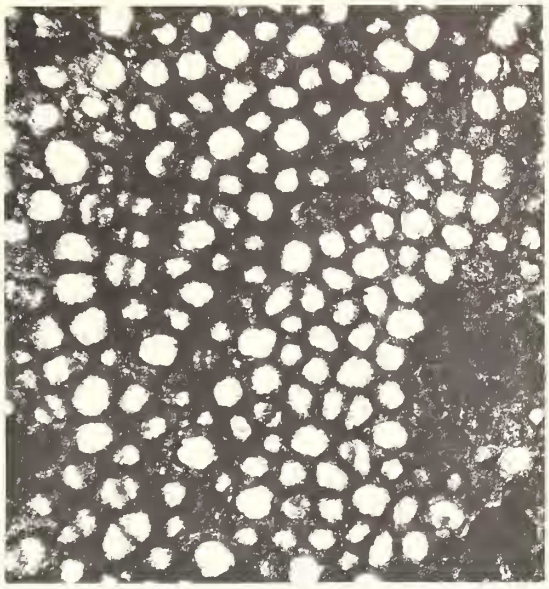

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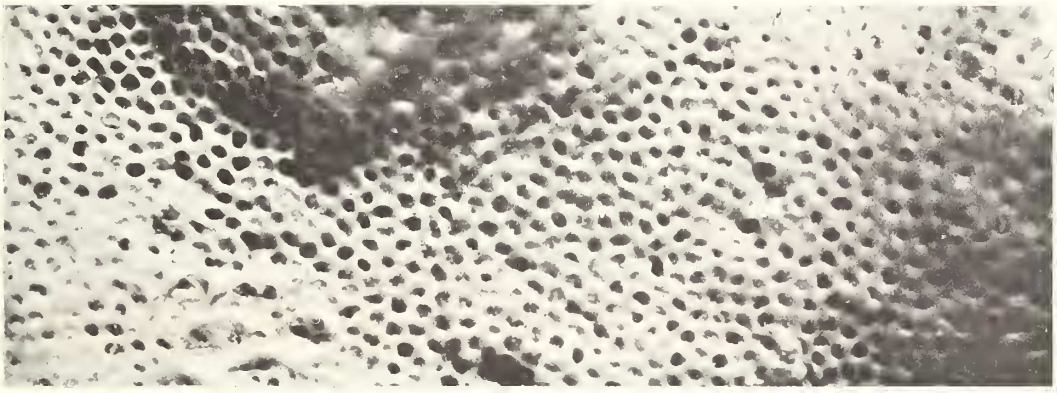

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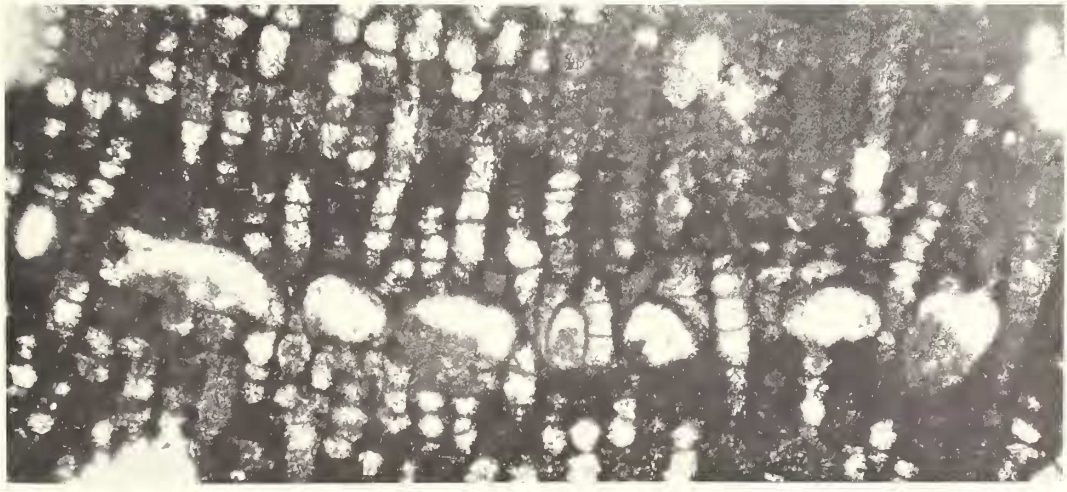

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ELLIOTT, *Neosolenopora*

horizontal courses or series, like those of sporangia or conceptacles in crusting Corallinaceae, and I interpret them as evidence of definite solenoporacean reproductive structures.

The smallest of these is oval in section, 0·182 mm high by 0·109 mm diameter. It originates in one tubule and is conspicuously different to the normal rectangular, presumed vegetative, cells. It shows as a swollen structure wider than the tubule, and bounded by a dark cell-wall of 0·009–0·014 mm thickness. Within the calcite filling are several circular bodies of about 0·036 mm diameter.

To left and right of this single structure, others occur along a curved row representing an old surface or subsurface of the growing plant. Almost all these have the same height, but they vary greatly in width. From this, and from the irregularity of their upper and lower surfaces, they appear to have been formed by the fusion, in different examples, of two or of several of the single bodies described above. All are bounded by outer walls, though none show the circular bodies seen within the single example.

A second row of similar structures is seen elsewhere in the same specimen. Here a multiple example, extending across five tubule-rows, contains many circular bodies like those in the single one described, and there are traces in the contents of some other examples.

A single example is exceptional in size and form; it is heart- or shield-shaped in section, with diameter of 0·218 mm and with a minimum height of 0·300 mm measured at the indentation. The height is 0·337 mm to one side of this, and on the other, where it is prolonged into a tube-like projection, is 0·355 mm. The bottom half of the calcite-filled interior shows as an amorphous mass of the same grey as the small spherical bodies in the other examples. Although this exceptional cavity extends across two tubules, it is different from a simple 'double' example.

It seems difficult to explain these structures in any way other than that they are reproductive in origin, resembling the sporangia and conceptacles of the crusting Corallinaceae, and this is discussed in more detail below. In crusting corallines the plane of reproductive structures, at right angles to the vertical section which shows them in a curved row, usually shows them scattered irregularly. However, a similar cut in *Neosolenopora*, as interpreted by the circular tubule-sections, again showed the reproductive bodies in a row with the presumed third diameter as about 0·182 mm.

Holotype. A nodule from which three thin-sections have been prepared. Miocene, Vindobonian, Savignéan Falun; La Perchais Quarry, Tréfumal, south of Dinan, Brittany, France. Brit. Mus. (Nat. Hist.) Dept. Palaeont., reg. nos. V. 53652, a, b, c. Plate 21, figs. 1, 2, 4; Pl. 22, figs. 2–5.

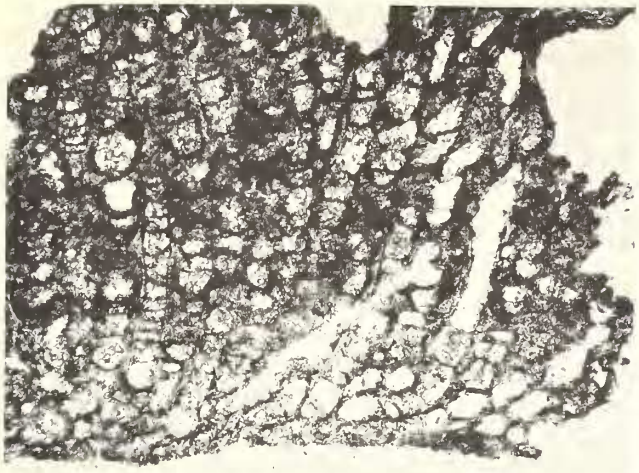
Paratypes. Two thin-sections cut from another nodule, same locality and horizon. Reg. nos. V. 51237, 51238. Pl. 22, fig. 1. A third nodule, not cut, V. 57125, Pl. 21, fig. 3.

DISCUSSION

N. armoricana seems similar to the type-species, *N. patrinii* from the Italian Helvetian. This was described and figured (as *Lithophyllum vinassai*) by Patrini (1932) and reviewed by Mastrorilli (1955), who emended the nomenclature. The most conspicuous difference is in the length of the ordinary cells; Mastrorilli gives dimensions for *N. patrinii* as 0·24–0·30 mm by 0·06–0·10 mm, whereas the corresponding dimensions for *N. armoricana* are 0·05–0·20 mm by 0·08–0·11 mm. Patrini's figures illustrate this clearly. They also show a hypothallial zone certainly thicker

EXPLANATION OF PLATE 22

Figs. 1–5. *Neosolenopora armoricana* sp. nov. Horizon and locality as Plate 21. 1, Thin-section, vertical cut of basal growth to show rudimentary hypothallus, ×46. V. 51238. 2, Thin-section, vertical section of single ovoid reproductive body, containing presumed tetraspore bodies, ×122. V. 53652c. 3, Thin-section, near-horizontal (transverse) cut showing a reproductive body near right-hand margin, ×46. V. 53652b. 4, Thin-section, vertical cut to show multiple reproductive body with presumed tetraspore bodies, ×122. V. 53652c. 5, Thin-section, vertical cut of reproductive body, presumed sexual, ?female, ×122. V. 53652c.



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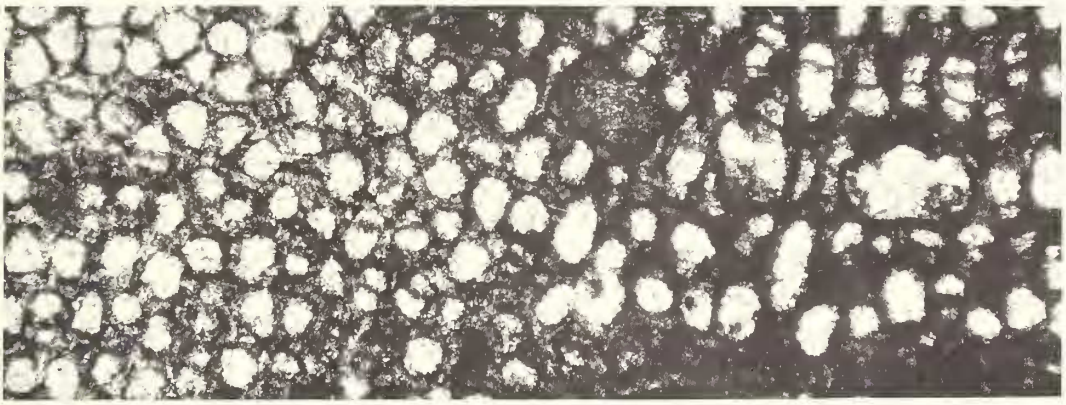

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than that in *N. armoricana*; the cell-differences seen in this may be due to a different angle of section to that figured in the present work, but this is difficult to evaluate. Clear rows of apparently calcite-filled reproductive structures, single, double, and multiple, are shown by him (op. cit., pl. 1, figs. 3, 5) but cannot be seen in as much detail as now given for *N. armoricana*.

The interpretation of the reproductive structures in *Neosolenopora* necessitates a comparison with those known in the Corallinaceae. At first sight the single bodies suggest the discrete sporangia of *Archaeolithothamnium*, and the larger bodies the conceptacles of a genus such as *Lithothamnium*. However, in living crusting corallines, conceptacles develop as structures *sui generis*, beginning as a heightening of adjacent cells over a limited area, a process facilitated by the lamellar (horizontal) cell-arrangement, and then developing to a box-structure containing the sporangial bodies. It is easy to see that this would not readily occur in *Neosolenopora* where the cell-arrangement is columnar and irregularly septate. In the single example described, the reproductive body is swollen by reference to normal tubule-diameter, encroaching on adjacent tubule-space. If, as in the crusting corallines, seasonal-physiological factors influenced the development of reproductive structures as a sporadic surface or subsurface phenomenon, then developing reproductive bodies in adjacent tubules would inevitably become modified. For this reason, the larger reproductive bodies are to be regarded not as conceptacles, but as fused sporangia, and this is indirectly confirmed by their varying width, depending entirely on the number of component merged sporangia.

The sporangia of *Archaeolithothamnium*, and the great majority of the conceptacles of *Lithothamnium*, *Lithophyllum*, and their allies, contain asexual tetraspores. The sexual structures in these genera, male and female, containing either antheridia or carposporangia are fewer, but are of general conceptacle pattern; they can sometimes be recognized in fossils (Conti 1946, 1950; Elliott 1970; Lemoine 1962, 1971; Segonzac 1970). If, as seems likely, solenoporoid reproduction was somewhat similar to that of the Corallinaceae, and also bearing in mind the necessarily different development of the sporangia already discussed for *Neosolenopora*, what form would the sexual structures take?

The solitary candidate seen for this interpretation in *Neosolenopora* is the large heart-shaped body already described. Size and shape preclude it from being an ordinary 'double sporangium', and the long neck is typical of some sexual conceptacles in Corallinaceae. It could be that the space needed for development of sexual as opposed to asexual development was in a tubular, columnal cell-arrangement only achieved by vertical development: the normal vegetative cells vary much in this dimension. It seems quite likely then, that this may have been a sexual reproductive body. The large amount of presumed organic residue in the lower part, of the same microscopic appearance as the material of the circular spore-packets in the normal asexual sporangia, suggests that it was possibly a female structure, since in my experience carpogonia leave more indication in the fossil state than antheridia. But this is speculation.

The complete absence or rare occurrence of very doubtful reproductive structures in Solenoporaceae, through Palaeozoic, Mesozoic, and Tertiary, has already been noted. If indeed comparable organs to those of the Corallinaceae were in most

Solenoporaceae external, non-calcified, and presumably deciduous, this would be in accord with the usual solenoporacean columnar cell-structure. The alleged reproductive bodies of *Solenomeris*, described by Rao and Varma (1953), and figured by Maslov (1956) and myself, were discounted by me (Elliott 1965), but some workers, e.g. Boulanger and Poignant (1969), are convinced of their sporangial nature and may well be correct in this. They are, however, not so easily reconcilable with the structures known in the Corallinaceae as are those now described for *Neosolenopora*.

I have elsewhere put forward the suggestion that the Solenoporaceae, individual species of which occasionally achieved typical corallinacean features such as calcified reproductive structures and differentiated hypothallial cell-layers, were precluded from a marked evolutionary development along these lines by cell-size and pattern, this possibly reflecting a different algal chemistry to that of the Corallinaceae (Elliott 1965). The rather different ecological behaviour of the two groups is also significant, the Corallinaceae achieving a successful exploitation of the coral-reef environment in the Tertiary never equalled by Palaeozoic or Mesozoic Solenoporaceae. *Neosolenopora* seems easily to be the most, if indeed not the only, successful solenoporoid in attaining a reproductive evolution leaving a calcified record as in Corallinaceae. It is of interest that, so far as is known, it is the very last of its kind, and evolved well after the Corallinaceae were established and dominant.

REFERENCES

BOULANGER, D. and POIGNANT, A.-F. 1969. Sur les nodules algaires du Lutétien supérieur de Sainte-Marie-de-Gosse (Landes). *C.r. somm. Séanc. Soc. géol. Fr.*, 1969, fasc. 4, 109–110.

CONTI, S. 1946. Le Corallinacee del calcare miocenico (Leithakalk) del bacino di Vienna. *Pubbl. Ist. Geol. Univ. Genova*, (A) Quad. 1–2, 31–68.

—— 1950. Alghe corallinacee fossili. Ibid., (A) Quad. 4, 156 pp.

ELLIOTT, G. F. 1965. Tertiary solenoporacean algae and the reproductive structures of the Solenoporaceae. *Palaeontology*, **7**, 695–702.

—— 1970. *Pseudaethesolithon*, a calcareous alga from the Fars (Persian Miocene). *Geologica romana*, **9**, 31–46.

—— 1972. *Cretacicrusta* gen. nov., a possible alga, from the English Cretaceous. *Palaeontology*, **15**, 501–503.

LEMOINE, M. 1962. Remarques sur la reproduction sexuée des *Archaeolithothamnium*. *Bull. Soc. phycol. Fr.*, no. 7 for 1961, 8–9.

—— 1971. Remarques sur la reproduction des algues calcaires fossiles Mélobésiées, la systématique et la phylogénie. *Revue algol.* (n.s.), **10**, 152–161.

MASLOV, V. P. 1956. Fossil calcareous algae of the U.S.S.R. *Trav. Inst. Sci. geol. Akad. nauk SSSR*, **160**, 1–301. (In Russian.)

MASTRORILLI, V. I. 1955. Sui noduli fossiliferi di M. Vallassa (Appennino Pavese). *Atti Ist. geol. Univ. Pavia*, **6**, 61–74.

ÖPIK, A. and THOMPSON, P. W. 1933. Über Konzeptakeln von *Solenopora*. *Publ. geol. Instn Univ. Tartu*, no. 36, 1–8.

PATRINI, P. 1932. Su di un nuovo litofillo miocenico. *Riv. ital. Paleont.* **38**, 53–60.

PIA, J. 1927. Thallophyta. *In* M. HIRMER, *Handbuch der Paläobotanik*, Munich–Berlin.

RAO, S. R. NARAYANA and VARMA, C. P. 1953. Fossil algae from the Salt Range. *Palaeobotanist* (*Lucknow*), **2**, 19–23.

SEGONZAC, G. 1970. Réflexions sur le genre *Palaeothamnium* Conti (Algues mélobésiées). *Bull. Bur. Rech. géol. min. Paris*, (2) Sect. IV no. 4, 1–9.
VIALLI, V. 1938. Su taluni fossili liassici del Monte Peller. *Studi trent. Sci. nat.* **19,** 52–68.
WOOD, A. 1944. Organs of reproduction in the Solenoporaceae. *Proc. geol. Ass., Lond.* **55,** 107–113.

G. F. ELLIOTT
Department of Palaeontology
British Museum (Natural History)
London, SW7 5BD

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